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The development of the embryo and seedling of Dioscorea villosa

PEARL MABRY SMITH

(WITH PLATES 31–34)

INTRODUCTION

According to the standard manuals, *Dioscorea villosa* L. is the only North American species of the Dioscoreaceae, a family that is mainly tropical and subtropical in distribution. Bartlett (1910), however, considers the name *D. villosa* at once a misnomer and a possible source of confusion and error, and proposes that it be dropped. In his classification, the Dioscoreae of the United States are referred to five separate species; the one treated in the present paper he calls *D. paniculata* Michx.

The early discussions of the embryos and seedlings of members of this family are confined to the mature embryo and its behavior in germination, and were prompted chiefly by taxonomic considerations. Dutrochet (1835) says that the embryo of *Tamus communis* is at first globular, then pear-shaped; the slender part is the cotyledon, the swollen part the body of the embryo. He describes two cotyledons: the one, conical in form, remaining within the seed during germination; the other, so closely applied to the globular part of the embryo that it is distinguishable only after germination. The larger cotyledon persists until the middle of summer. Dutrochet also describes the structure of the aerial stem, whose fibro-vascular bundles are of the monocotyledonous type, but arranged in a ring. He thinks that this apparent mingling of monocotyledonous and dicoty-

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ledonous characters indicates that the genus is intermediate between the two classes, although he refers it to the Asparageae. Endlicher (1836, p. 157) notes a resemblance in stem structure between *Tamus* and *Aristolochia*.

Jussieu (1839) finds a structure corresponding to the "second cotyledon" of Dutrochet in the embryos of *Dioscorea villosa*, *D. cordifolia*, and *Rajania hastata*. However, he thinks it to be not a cotyledon, but a sheath formed by the growth of the cotyledon, its development being coincident with the elongation of the cotyledonary limb. In his classification the genera in question are placed among the Asparageae.

Beccari (1870*a*), in agreement with Dutrochet, concludes from his examination of the embryos of *Dioscorea bonariensis*, *D. brasiliensis*, *D. sinuosa*, *Rajania cordifolia*, *Tamus communis*, and *Trichopus zeylanicus* (*Trichopodium zeylanicum*) that the organ in question is a rudimentary cotyledon; he finds it present, with some variation in shape and size, in all the species named. Beccari also studied the germination of *D. bonariensis;* his description and figure agree substantially with Dutrochet's account of the process in *Tamus communis*.

The textbook of Le Maout and Decaisne (1873, p. 794) contains a figure of a longitudinal section of a germinating seed of *Tamus communis*, which shows very clearly the structures described by Dutrochet and others.

According to the view advanced by Strasburger (1872, pp. 317, 318), monocotyledons were derived from dicotyledons by the loss of one cotyledon. Obviously, if the Dioscoreaceae can be held to constitute a transition stage, or transition stages, between monocotyledons and dicotyledons, the "second cotyledon" might well represent a stage in the degeneration of one of the cotyledons of the latter group. Stimulated by these considerations, Solms-Laubach (1878) studied the embryology of *Dioscorea pyrenaica* and *Tamus communis*, the latter in some detail, but his results did not convince him that a second cotyledon was formed. However, he found a type of embryological development quite different from that which, since the work of Hanstein (1870), had been considered characteristic of monocotyledons. The growing point of the stem appears early in a terminal or nearly terminal position,

from which it is pushed aside by the development of the lateral true cotyledon. The so-called second cotyledon is, he thinks, merely a sheath. Both cotyledon and sheath are developed, however, according to Solms-Laubach, from a ring-shaped primordium.

Bucherer (1889) points out the additional fact that in *Tamus* not only the first secondary leaf, but all the secondary leaves, have similar sheaths. He also describes the anatomy of the mature embryo, and the processes of germination and of tuber formation. His account of the germination of the seed does not differ from the accounts of his predecessors.

MATERIAL AND METHODS

Material was collected in the vicinity of Madison, Wisconsin, at intervals of two or three days during the months of June, July, and August, 1913 and 1914. The flowers were fixed entire; when the ovules became sufficiently large, they were removed from the capsules before fixing. Later, the embryos were dissected out of the young seeds and then fixed. Difficulty was experienced in inducing the seeds to germinate, but germination was finally secured by keeping the seeds in soil out of doors all winter and bringing them into the greenhouse in the spring.

Strong and medium chrom-osmic-acetic acid solutions were used for all material of the embryo-sac and embryo which was to be sectioned; the stronger solution proved the more satisfactory. For embryos to be mounted *in toto* Carnoy's solution was used; for the seedling, a chrom-acetic acid solution, containing three tenths of a gram of chromic acid and seven tenths of a gram of acetic acid in each hundred grams of the solution, gave good results. The usual methods of hardening and embedding in paraffin were followed. Microtome sections were cut from five to seven microns thick.

Material containing embryo-sacs or early embryonic stages was stained with Flemming's triple stain. For the study of the later stages in embryo-development, Heidenhain's iron-alum-haematoxylin gave the best results. Some of the mature embryos were stained *in toto* with Delafield's haematoxylin. Staining with safranin and Lichtgrün proved useful in differentiating the tissues of the seedling.

THE EMBRYO-SAC

Two anatropous ovules are borne in each cell of the three-celled ovary and are pendulous on rather short funiculi. Beccari (1870*b*) figures the ovules in *Trichopus zeylanicus* as turned towards the axis of the pistil, but in *Dioscorea villosa* they are turned away from the axis.

At the time when the embryo-sac is fully organized (FIG. 1), the three antipodal cells have already begun to degenerate and fusion of the polar nuclei has taken place. Before the egg divides, its cytoplasm is highly vacuolate, and the nucleus occupies a position either approximately in the center or at the distal end of the cell. Both synergids persist, at least in some cases, until after the first division of the egg. When the embryo is somewhat older, only one structure is found beside it which I take to be a synergid. This structure (FIG. 5, *s*) sometimes forms a beak with faint longitudinal striations, which extends into the micropyle and corresponds closely in form and appearance with the "Fadenapparat" first described by Schacht (1856).

THE EMBRYO

The first division of the egg takes place only after several nuclear divisions have occurred in the endosperm. In an embryo-sac containing a two-celled embryo a count of the endosperm nuclei shows that five divisions have taken place, and the general appearance of the endosperm in other similar cases indicates that about the same number of divisions has occurred. In all cases observed, the plane of the first division of the egg is oblique (FIG. 2), approaching in a few instances the vertical (FIG. 4) or the horizontal (FIG. 5). The corresponding division is in an oblique plane in *Tulipa Gesneriana* (Ernst, 1901), and occasionally in *Avena fatua* (Cannon, 1900), and *Aglaonema* (Campbell, 1900). But in most monocotyledons, so far as has been reported, the plane of this division is transverse, as for instance in such forms as *Sagittaria variabilis* (Schaffner, 1897), *Lilaea subulata* (Campbell, 1898), and *Lilium philadelphicum* (Coulter, 1897). A transverse first division is found also in *Tamus communis* (Solms-Laubach, 1878), another of the Dioscoreaceae. The cells pro-

duced by this division in *Dioscorea villosa* are usually of about the same size (FIG. 4), but sometimes the basal cell is larger (FIG. 2). On account of the flattened shape of the seed it is possible to section the ovules always in the same plane. All figures of sections of the embryo are drawn from median longitudinal sections which are vertical to the plane of the cotyledon and which consequently afford a fair basis for comparison. In no case is a large vesicular basal cell formed, such as has been described in the embryos of the Najadaceae and Alismaceae.

The second division occurs in the basal cell, at right angles to the first wall (FIG. 3). Next, the terminal cell divides (FIG. 4); the position of the wall formed as a result of this division varies: in some embryos it is in the same plane as that of the second division (FIG. 4); in others, it is at right angles to the second wall, as in the embryo shown in FIG. 5, in which the third wall is nearly in the plane of the section and therefore cannot be shown in the figure. By either method, four similar cells are formed, as is the case in a few monocotyledons which have a massive proembryo rather than one of the filamentous sort that was formerly considered typical for the class. Quadrant formation has been observed in three genera of monocotyledons, *Lysichiton* (Campbell 1900), *Lilium* (Coulter, 1897), and *Erythronium* (Schaffner, 1901). It can hardly, however, be considered typical for the Dioscoreaceae, since in *Tamus communis* (Solms-Laubach, 1878) a filamentous three-celled proembryo has been described.

The next division may take place in one of the two distal cells or in one of the two basal cells. In the embryo shown in FIG. 5, the nucleus of one of the distal cells of a four-celled embryo is dividing; the wall separating the two distal cells is, as already noted, so nearly parallel to the plane of the section that it cannot be indicated in the figure. The spindle is at a lower focus than the resting nucleus shown.

In most cases, the second of the two distal cells of the four-celled stage now divides, so that a six-celled embryo is formed. Up to this time the embryo has not materially increased in size, but from now on there is a gradual growth. At the eight-celled stage (FIG. 6) the embryo is already noticeably larger, the size of the individual cells at this time being approximately equal to

that of the cells at the six-celled stage. At the sixteen-celled stage, the embryo assumes one of two typical shapes, each of which has been observed in several cases: it may be either elongated (FIG. 7), or nearly globular (FIG. 8). The exact sequence of divisions cannot be followed with any certainty after the eight-celled stage, nor is it possible to trace the development of the organs of the full-grown embryo from particular cells.

As the embryo develops a region is differentiated at the apex in which division is especially active, as indicated by the smaller size of the cells (FIG. 9, *m*). An elongation of the embryo, together with the increased rate of growth in its apical region, renders it a little later roughly pear-shaped (Fig. 10). The suspensor is now definitely marked off from the rest of the embryo (FIG. 10, *s*), and reacts differently to stains in this and succeeding stages. Now, too, the dermatogen is differentiated except on the side from which the first secondary leaf is to develop (FIG. 10, *l*; compare also FIG. 11, *l*). An embryo of the age of that shown in FIG. 10 bears a fairly close resemblance to one of *Lilium philadelphicum* figured by Coulter (1897, *pl. 34, f. 31*). Solms-Laubach (1878) shows no embryo of *Tamus communis* or of *Dioscorea pyrenaica* at a similar stage of development. Older stages than that of my FIG. 11 are represented in his figures only by drawings of surface views of whole embryos. According to Solms-Laubach's description the original terminal arch of the embryo becomes somewhat flattened and laterally displaced by the growth of one side of the embryo. From the flattened portion the plumule develops, surrounded by a ring-shaped wall of tissue. In my preparations of *D. villosa*, it appears clear that the lateral swelling shown at FIG. 11, *l*, which probably corresponds to that described by Solms-Laubach, is the primordium of the first secondary leaf, whose further development is shown in FIGS. 15–24. The growing point of the stem lies in the axil of the first secondary leaf, and it is obvious that both these structures are lateral in origin. The cotyledon (FIG. 11, *c*) develops in a terminal position. In *Tamus communis* and *Dioscorea pyrenaica*, according to Solms-Laubach, first the cotyledon and then the sheath develop from opposite points in the ring-shaped primordium, and are hence of lateral origin.

A careful study of serial sections of embryos of *Dioscorea villosa*, corresponding in size to those figured by Solms-Laubach, shows that no ring-primordium is formed, but that the first secondary leaf and cotyledon originate as limited areas of meristematic activity in an embryo which is still meristematic in all its parts; there is a very great increase in the size of the embryo as a whole after the first secondary leaf and the cotyledon have begun their development (FIGS. 15–24, all drawn on the same scale). The growing point of the stem consists merely of a group of cells in the axil of the first secondary leaf, and remains quite undifferentiated (FIG. 12, *g*) until germination occurs. The growth of the first secondary leaf is more vigorous at the start than that of the cotyledon (FIG. 15); but the latter soon begins to elongate rapidly, then expands to form a foliaceous structure which, in the fully-developed embryo, is peripherally very thin and flat, but is much thicker in the middle portion and at the base (FIGS. 13, 24). The first secondary leaf continues to swell out, then arches over and finally covers the growing point of the stem (FIG. 24). In the full-grown embryo, the edges of the base of the cotyledon extend for a short distance over the first secondary leaf, but by no means cover it (FIG. 13). A strikingly different structure has been described for embryos of other members of the Dioscoreaceae, which have a distinct sheath entirely covering the first secondary leaf. Beccari (1870*a*) finds this sheath entire in the genera *Dioscorea* and *Trichopus*, and two-parted in *Rajania* and *Tamus;* Solms-Laubach (1878) says that it is entire in *Testudinaria*. The short, thick suspensor persists to the time of the maturity of the seed (FIG. 13, *s*).

A vascular system, consisting of procambium strands, is present in the full-grown embryo of *Dioscorea villosa*. Cross-sections through the hypocotyl show a solid plerome cylinder which becomes a hollow cylinder at the base of the cotyledon. The hollow cylinder opens out into a trough-shaped mass as it passes into the cotyledon, then branches into three main bundles, which, in turn, branch profusely (FIG. 13). The first secondary leaf has a well-marked median bundle and two rather weakly developed lateral bundles. Bucherer (1889) describes but one vascular strand in the cotyledon of *Tamus communis;* in *Tamus*, however, the

cotyledon is tongue-shaped and not flattened. Bucherer also says that the primary root is endogenous and breaks through several rows of parenchyma cells when the seed germinates. No evidence of this condition has been found in *D. villosa*. There are no parenchyma layers outside the well-defined root-cap, which lies in immediate contact with the suspensor.

THE ENDOSPERM

As has been said, the polar nuclei fuse early and the primary endosperm nucleus undergoes several divisions previous to the first division of the egg; the nuclear divisions in the endosperm are simultaneous. The young embryo is at all times closely invested with a thick layer of endosperm cytoplasm. The endosperm makes rapid inroads on the nucellar tissue, using up all of it excepting two layers at the sides of the embryo-sac cavity and thicker masses at the chalazal and micropylar ends before cell division begins in the endosperm. Cell formation in the endosperm begins when the embryo has reached about the stage shown in FIG. 10. Tissue is formed at first throughout the whole of the cavity; later, but before the maturing of the seed, enough of this tissue is dissolved to form a large fissure in the central part of the seed which affords room for the rapid growth of the cotyledon at the time of germination. The cells of the endosperm contain abundant reserves of hemicellulose, protein, and oil. Dutrochet (1835) and Beccari (1870*a*) refer to the food material in the seeds of various Dioscoreaceae as "perisperm," but in *Dioscorea villosa* the material is clearly endosperm.

Formation of endosperm tissue is accompanied by, and is perhaps responsible for, certain changes in the contour of the seed and in the position of the embryo. When cell walls begin to form in the endosperm, nuclear division continues and is especially active in the region opposite the funiculus and adjacent to the embryo with the final result that this portion of the seed becomes proportionately larger than the other parts. As a result of this one-sided growth, the embryo, whose long axis at first corresponds to the long axis of the embryo-sac, comes to lie with its axis at an angle of approximately forty-five degrees to the long axis of the seed.

THE SEEDLING

In the mature seed, the embryo is very small in proportion to the size of the seed. On germination the cotyledon increases rapidly in size (FIG. 28, *c*), filling the entire fissure which has been referred to as formed within the endosperm, and remaining within it. The basal part of the cotyledon elongates, forming a trough-shaped petiole in whose hollow the first secondary leaf lies. The primary root elongates rapidly and soon begins to give off secondary roots. The first secondary leaf elongates, then arches itself until its tip becomes free from the seed coats. Beccari (1870*a*) says that in *Dioscorea bonariensis* the first secondary leaf is bent over so that the upper surface of the lamina lies against the petiole until the entire leaf emerges. In *D. villosa* the leaf is not bent over while in the seed, but assumes the position described by Beccari on freeing itself from the seed and retains it until it is well above ground. In the seedling illustrated in FIG. 28, the second, third, and fourth secondary leaves have already begun to develop.

The three bundles of the cotyledon fuse in the petiole to form a single massive bundle (FIG. 27) which extends the entire length of the petiole, is clearly recognizable in the hypocotyl (FIG. 26, *t*), and forms one of the poles of the tetrarch root (FIG. 25, *t*). This condition differs from that in *Tamus*, in which, according to Miss Sargant (1903), the symmetry of the root stele depends upon plumular traces alone. No traces of cambium, such as often occur in monocotyledonous seedlings, were found. Each secondary leaf has three bundles. Excepting the traces from the second and third secondary leaves, no vascular strands are present in the seedling that are not represented in the embryo by procambial tissue.

There are eight bundles in the hypocotyl (FIG. 26). The largest one (*t*) is continuous with the cotyledonary bundle. Of the remaining bundles, the three largest (*lt*) are continuous respectively with the three bundles of the first secondary leaf. The hypocotyl is short, as in most monocotyledons, so that the bundles of the hypocotyl converge rather rapidly as they enter the root and are consequently difficult to follow. It is evident, however, that branching of the phloem groups of the four main bundles

occurs, and that the branches fuse in pairs to form the phloem groups of the root. At the same time, a rearrangement of the xylem groups takes place, with the result that the protoxylem, which is external in the hypocotyl, becomes internal in the root.

CONCLUSIONS

Apparently the early divisions in the embryo of *Dioscorea villosa* have no very definite relation to the formation of organs or to the constitution of the embryo, since no important differences are found among the ripened embryos which might correspond to the observed differences in the plane of the first division or in the shape of the proembryo.

Widely accepted generalizations on the embryology of monocotyledons and dicotyledons have been based on cases such as *Sagittaria* and *Capsella* in which a filamentous proembryo is formed whose terminal cell gives rise to the cotyledon in monocotyledons and to the stem primordium in dicotyledons. However, as Coulter and Land (1914) have pointed out in the case of *Sagittaria*, the origin of organs from particular cells of filamentous proembryos has been assumed rather than proved. Moreover, a number of genera, both of monocotyledons and dicotyledons, have now been investigated in which the proembryo is massive. In several monocotyledonous genera, including *Zannichellia* (Campbell, 1897), *Lilaea* (Campbell, 1898), *Sparganium* (Campbell, 1899), *Avena* (Cannon, 1900), and sometimes *Limnocharis* (Hall, 1902), both cotyledon and growing point are found to originate from the terminal segment. However, a considerable amount of growth, resulting in a mass of tissue, must occur in the embryo before actual differentiation of organs takes place. If the positions of the primordia of the cotyledon and stem on this mass of tissue can be said to be terminal or lateral, this difference might serve as a basis for the distinction between monocotyledonous and dicotyledonous embryos. Unfortunately, it is at just this period of development that gaps in embryological studies are usually found. If position of origin be considered the criterion, the embryo of *Dioscorea villosa* is strictly monocotyledonous.

Lyon (1901) has advanced the view that an area extending entirely around the axis of the embryo is potentially cotyledonary.

The maximum development in this area takes place at the point or points that are in the most favorable position to function; in monocotyledons maximum development occurs on only one side, while in dicotyledons equal growth occurs at two points diametrically opposite each other. This notion has been further developed by Coulter and Land (1914) in connection with their work on some of the South African Liliaceae, particularly *Agapanthus*. Coulter (1915) even extends the generalization to gymnosperms. According to his view, a variable number of primordia appear on the cotyledonary ring; one, two, or more of these develop, the growth of the others being checked, principally by the growth of other organs of the embryo. As I have pointed out, no cotyledonary ring was observed at any time in the embryo of *Dioscorea villosa*, although such a structure has been described for *D. pyrenaica* and *Tamus communis* (Solms-Laubach, 1878). The two primordia that do appear in *Dioscorea villosa* develop into the cotyledon and the first secondary leaf respectively. The only way in which this case can be made to fit Coulter's theory is by assuming that the vigorous development of the first secondary leaf has entirely checked the development of the cotyledonary zone except at one point. However, the figures of Solms-Laubach (1878) indicate that the development of the first secondary leaf is just as vigorous in *Tamus*. I have no explanation to offer of the entire absence in *D. villosa* of a sheath covering the first secondary leaf, which is so prominent a feature in the embryos of other Dioscoreaceae.

There is so much diversity of opinion in regard to the phylogenetic significance of seedling anatomy that it seems hardly worth while to discuss the question to any extent in connection with *Dioscorea villosa*. Miss Sargant (1903) considers the tetrarch root such as is found in *D. villosa* primitive; however, in her opinion, this form of root structure is associated with the early development of the plumule which is characteristic of climbers. On the other hand, Hill and De Fraine (1913) consider diarch root structure primitive, but think that the root structure in any given case is largely dependent upon the size of the seedling. The seedling of *D. villosa* is small so that the formation of a tetrarch root cannot be accounted for on the basis of the size of the seedling. The

plant is a climber, however, and the structure of the root might be explained on that ground, thus losing its phylogenetic significance.

SUMMARY

1. The plane of the first division of the egg is oblique.

2. A spherical four-celled proembryo is formed.

3. The first secondary leaf is the first organ of the embryo to be differentiated. The growing point of the stem consists, up to the time of germination, of a group of cells in the axil of the first secondary leaf. Both structures are lateral in origin.

4. No "cotyledonary ring" was observed. The cotyledon originates in a terminal position.

5. No structure which is in any way comparable to a second cotyledon is present; the sheath which is described as covering the plumule in other Dioscoreaceae is wanting.

6. Abundant endosperm is present in the seed.

7. The growing point of the stem begins to give off secondary leaves soon after the seed germinates.

8. The root of the seedling is tetrarch; the hypocotyl is polyarch.

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UNIVERSITY OF WISCONSIN

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Description of plates 31-34

With the exception of FIG. 28, all drawings were made with an Abbé camera lucida, the drawing being at the level of the base of the microscope. Leitz oculars and objectives were used: FIG. 1, ocular III and objective 7; FIGS. 2–9, ocular III and objective 1/16; FIGS. 10–12, ocular I and objective 7; FIG. 13, ocular I and objective 3; FIGS. 14–24, ocular I and objective 4; FIGS. 25–27, ocular I and objective 6. The drawings have been reduced one fourth in reproduction.

PLATE 31

FIG. 1. Mature embryo-sac.

FIG. 2. Two-celled embryo.

FIG. 3. Three-celled embryo.

FIG. 4. Four-celled embryo.

FIG. 5. Four-celled embryo with one of the terminal cells in mitosis.

FIG. 6. Eight-celled embryo.

FIGS. 7, 8. Sixteen-celled embryos.

FIG. 9. Embryo somewhat older than those shown in FIGS. 7 and 8; region in which cell division has become especially active, *m*.

FIG. 10. Older embryo in which suspensor and body have become differentiated and which shows the first indication of the development of the primordium of the first secondary leaf, *l*; suspensor, *s*.

FIG. 11. Still older embryo in which the first secondary leaf, *l*, has begun development. The section was cut somewhat obliquely so that not all of the suspensor is shown; cotyledon, *c*.

PLATE 32

FIG. 12. Median longitudinal section through the fully-developed embryo, showing first secondary leaf, *l*, and the growing point of the stem, *g*.

FIG. 13. Surface view of the full-grown embryo; suspensor, *s*; first secondary leaf, *l*; cotyledon, *c*.

FIGS. 14–21. Series of outlines, all on the same scale, of median longitudinal sections of embryos, showing the development of the mature organs; first secondary leaf, *l*; cotyledon, *c*.

PLATE 33

FIGS. 22–24. Continuation of the preceding series, FIG. 24 showing the full-grown embryo.

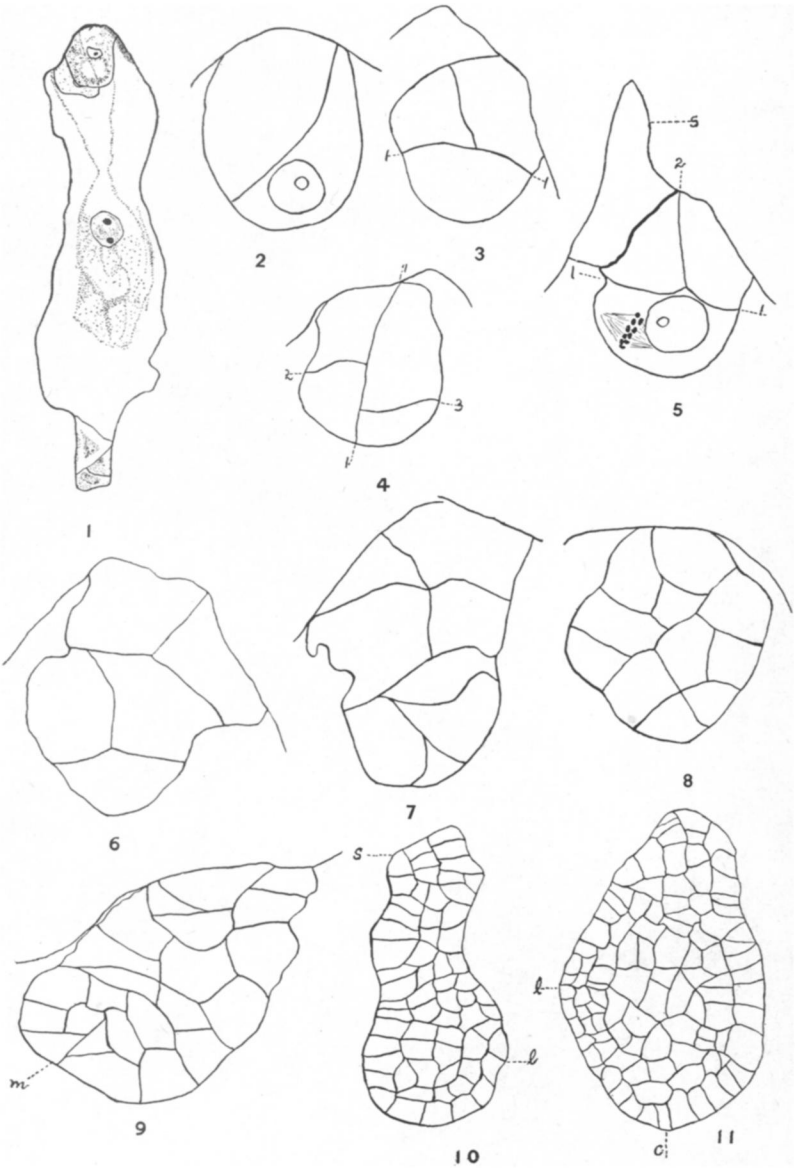
FIG. 25. Cross-section through the primary root of the seedling; cotyledonary trace, *t*.

PLATE 34

FIG. 26. Cross-section through the hypocotyl of the seedling; cotyledonary trace, *t*; traces from the first secondary leaf, *lt*.

FIG. 27. Cross-section through the base of the petiole of the cotyledon.

FIG. 28. Seedling dissected out of the seed; first secondary leaf, *l*; cotyledon, *c*.



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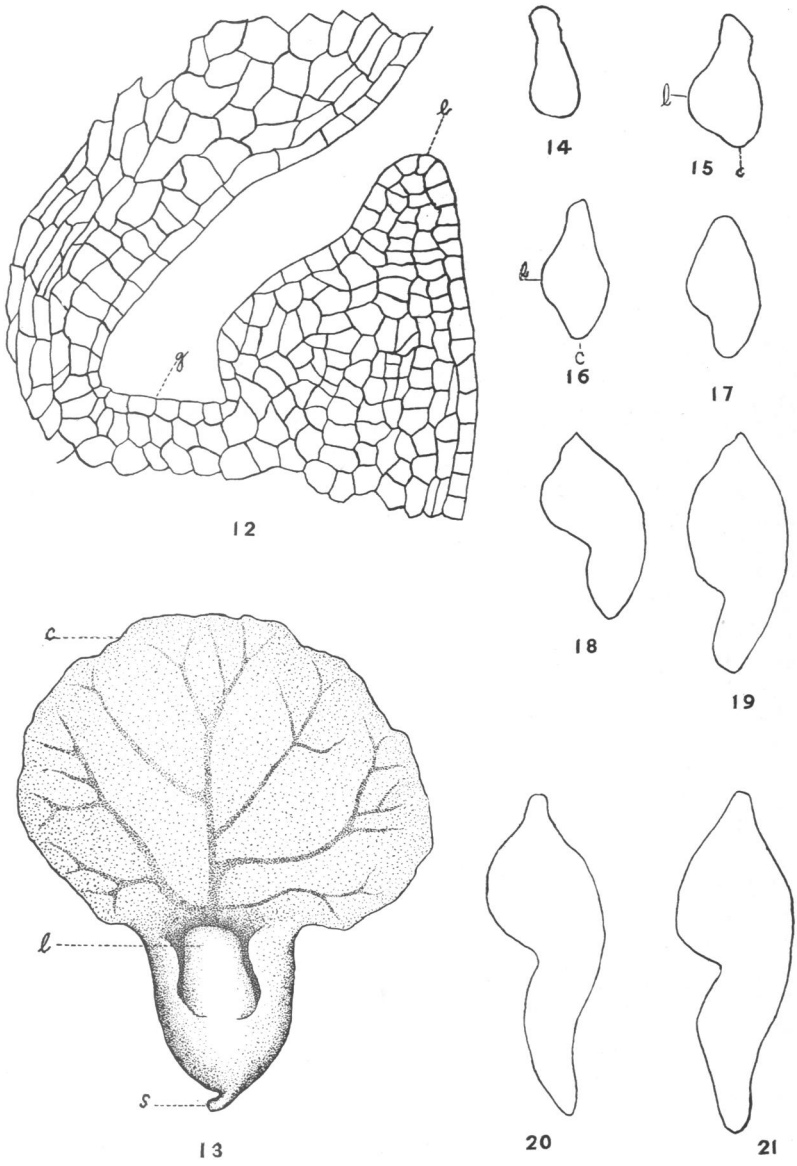

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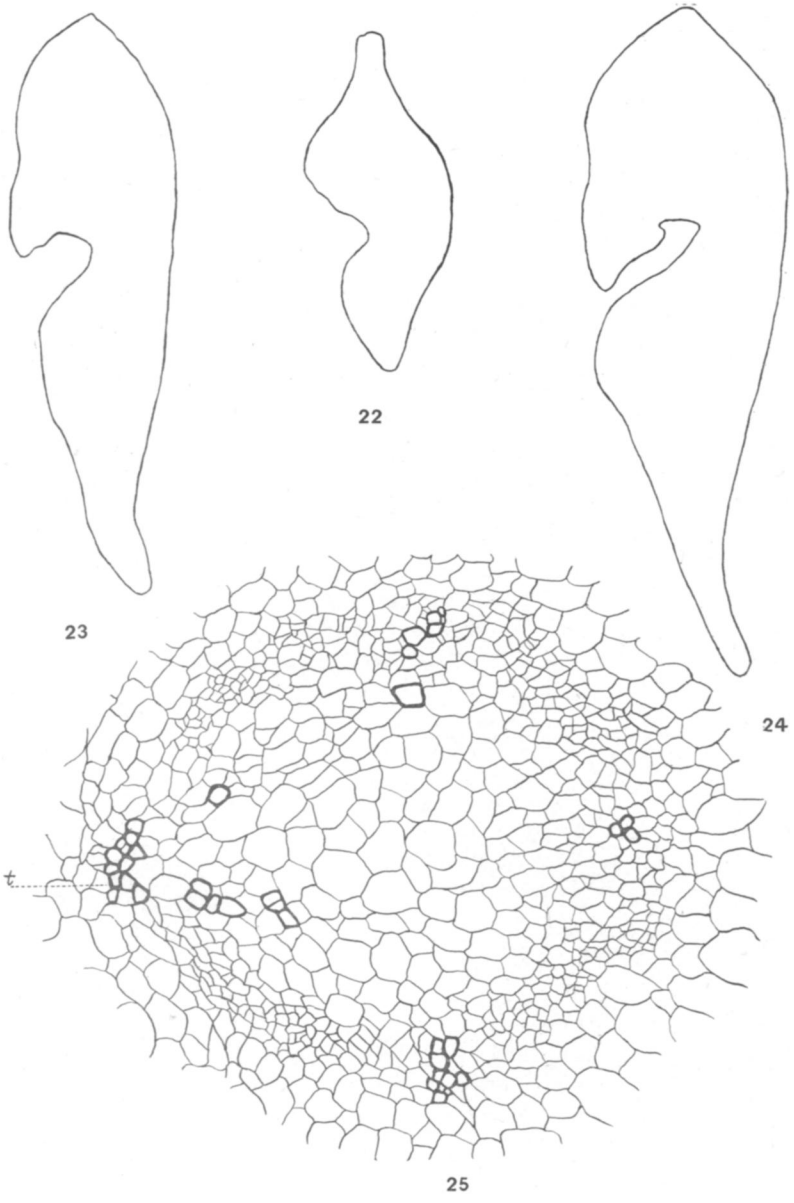

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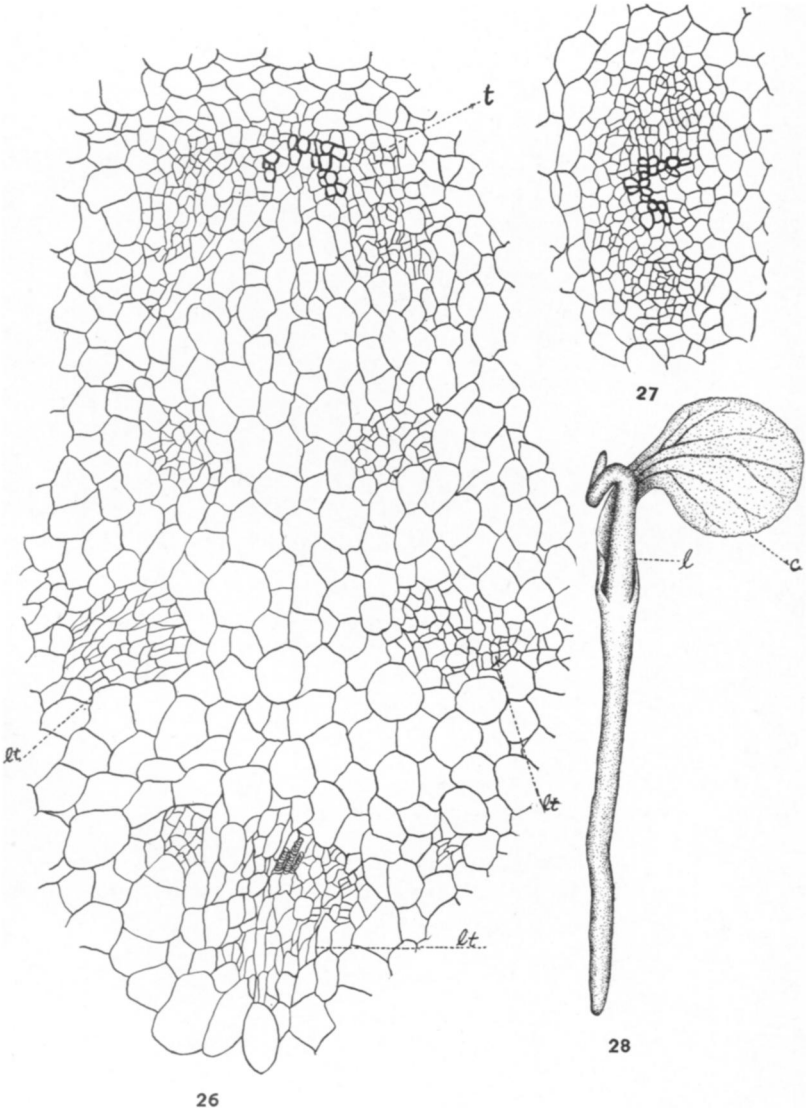

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